ACANTHEMBLEMARIA PAULA, A NEW DIMINUTIVE CHAENOPSID (PISCES: BLENNIOIDEI) FROM BELIZE, WITH COMMENTS ON LIFE HISTORY

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Abstract.—*Acanthemblemaria paula* is described from the barrier reef and outlying islands of Belize. The new species is the smallest member of the Chaenopsidae, reaching sexual maturity at 11.5 mm SL or smaller and attaining a maximum size of about 18 mm SL. In addition to its small size, it differs from all other *Acanthemblemaria* by its low number of dorsal-fin spines and distinctive head spination. Confusion of *A. paula* with *A. spinosa* led previous authors to erroneous conclusions about life history parameters of *A. spinosa* and larval recruitment in *Acanthemblemaria*.

In March 1987, we made shallow rotenone collections of fishes at the north end of Carrie Bow Cay, Belize, the site of a Smithsonian Institution field station since 1972. The purpose of these collections was to obtain otoliths for analysis of daily growth increments, and, thus, all specimens were fixed in 95% ethanol. Among the fishes collected were two tiny specimens of the chaenopsid genus *Acanthemblemaria* Metzelaar that we were unable to identify using the most recent generic revision (Smith-Vaniz & Palacio 1974). The ethanol-fixed material was less than ideal for systematic study, but led us to examine the extensive holdings of Belize *Acanthemblemaria* at the Field Museum of Natural History, collected and reported on by Greenfield & Johnson (1981). There, among 12 lots identified as *A. spinosa,* we found 50 additional specimens representing what we were then able to recognize as a previously undescribed species. Returning to Carrie Bow in March 1988, we discovered that the new species is quite common on the reef flat and has habits similar to those of *A. greenfieldi.* The new species is a diminutive form, the smallest known member of the Chaenopsidae, and this may partially explain how it has gone unrecog-nized, despite its residence in the environs of the very active Smithsonian research facility. As currently known its geographic distribution is restricted to Belize, and specimens were not present in material examined by Smith-Vaniz & Palacio (1974). In this paper we describe the new species and discuss its bearing on the conclusions of Greenfield & Greenfield (1982) concerning life history parameters of *A. spinosa* and habitat partitioning and larval recruitment in *Acanthemblemaria.*

Methods. —Counts and measurements largely follow the methods of Stephens (1963). Pore terminology is that of Smith-Vaniz & Palacio (1974), as modified by Johnson & Greenfield (1976) and Rosenblatt & McCosker (1988). Measurements were made with an ocular micrometer. All lengths are standard length (SL) unless stated otherwise. Vertebral and median fin ray counts were made from radiographs. Tooth and gill-raker counts were determined on cleared and stained specimens. Pore counts and head spine distribution were determined from scanning electron micrographs and whole specimens. Institutional abbreviations are as follows: ANSP, Academy of Natural Sciences of Philadelphia; FMNH,

Table 1.—Frequency distributions of fin-ray and vertebral counts in three species of *Acanthemblemaria*.

Species	Dorsal-fin spines						Dorsal-fin soft rays								Total dorsal-fin elements						
	18	19	20	21	22	$\bar{x}$	13	14	15	16	17	18	19	$\bar{x}$	33	34	35	36	37	38	$\bar{x}$
spinosa[1]	—	—	24	111	11	20.9	4	71	53	13	—	—	—	14.5	1	8	67	66	9	—	35.5
spinosa[3]	—	—	2	11	1	20.9	—	10	4	—	—	—	—	14.3	—	1	9	4	—	—	35.2
aspera[1]	—	1	59	53	8	20.6	—	5	29	68	18	—	—	15.8	—	—	16	49	48	7	36.4
aspera[2]	—	3	19	1	—	19.9	—	8	14	1	—	—	—	14.7	—	9	14	—	—	—	34.6
aspera[3]	—	—	6	13	—	20.7	—	2	14	3	—	—	—	15.0	—	—	6	12	1	—	35.7
paula[3]	13	72	29	1	—	19.2	—	—	1	35	54	12	1	16.8	—	—	18	60	25	—	36.1

Species	Anal-fin soft rays						Pectoral-fin rays				Segmented caudal-fin rays				
	21	22	23	24	25	$\bar{x}$	12	13	14	$\bar{x}$	11	12	13	14	$\bar{x}$
spinosa[1]	1	10	68	67	6	23.4	10	153	3	13.0	—	—	81	—	13.0
spinosa[2]	—	3	8	3	—	23.0	—	14	—	13.0	—	—	14	—	13.0
aspera[1]	—	11	50	48	11	23.5	11	133	5	13.0	2	92	34	1	12.3
aspera[2]	5	18	—	—	—	21.8									
aspera[3]	—	3	13	3	—	23.0	—	18	1	13.0	—	11	8	—	12.4
paula[3]	—	6	60	38	3	23.4	6	60	4	13.0	4	32	36	—	12.4

Species	Precaudal vertebrae				Caudal vertebrae					Total vertebrae					
	11	12	13	$\bar{x}$	28	29	30	31	$\bar{x}$	39	40	41	42	43	$\bar{x}$
spinosa[1]	81	4		11.0	3	18	52	12	29.9	1	18	54	12		41.4
aspera[2]		54	17	12.2	2	25	35	9	29.7		2	19	30	20	42.0
paula[3]		81	7	12.1	14	59	21		29.1		13	54	27		41.1

[1] Data from Smith-Vaniz & Palacio (1974).
[2] Data from Cartagena, Colombia population (Acero 1984).
[3] Original data based on specimens from Belize.

Field Museum of Natural History; USNM, United States National Museum of Natural History.

Acanthemblemaria paula, new species
Figs. 1, 2

Acanthemblemaria spinosa (in part, not of Metzelaar, 1919) Greenfield & Johnson, 1981.—Greenfield & Greenfield, 1982.

Diagnosis.—An *Acanthemblemaria* differing from all other members of the genus by its small size (sexually mature at <12 mm, largest specimen 18.4 mm) and low number of dorsal-fin spines (18–21, $\bar{x} = 19.2$) and further distinguished by the following combination of characters: supraorbital cirrus complexly branched; head spines well developed, those on frontals extending posteriorly beyond orbits in a triangular patch

reaching about two-thirds distance to dorsal-fin origin; anterior infraorbital with a few spines anteriorly, posterior infraorbital smooth.

Counts and measurements in mm of holotype.—Dorsal fin XX, 17; anal fin II, 24; pectoral fin 13. Standard length 15.9; head length 3.4; head depth 2.0; upper-jaw length 1.4; orbit length 0.6; snout length 0.5; interorbital width 0.5; predorsal length 1.9; preanal length 6.8; caudal-peduncle length 0.8; caudal-peduncle depth 0.9; orbital cirrus length 0.5; pectoral-fin length 3.3; longest dorsal-fin spine length 1.6.

Description.—Frequency distributions of fin-ray and vertebral counts are given in Table 1. Dorsal-fin spines 18–21 ($\bar{x} = 19.2$), soft rays 15–19 ($\bar{x} = 16.8$); total elements 35–37 ($\bar{x} = 36.1$). Anal fin II, 22–25 ($\bar{x} = 23.4$). Pectoral-fin rays 12–14 ($\bar{x} = 13.0$).

Fig. 1. *Acanthemblemaria paula*, new species, holotype, USNM 301835, male, 15.9 mm SL, Carrie Bow Cay, Belize.

Segmented caudal-fin rays 11–13 ($\bar{x} = 12.4$). Pelvic-fin rays I, 3. Vertebrae: precaudal 12–13 ($\bar{x} = 12.1$); caudal 28–30 ($\bar{x} = 29.1$); total 40–42 ($\bar{x} = 41.2$).

Body very slender and elongate, comparable to that of *Acanthemblemaria chaplini,* the most elongate and slender species of the genus; head depth 7.3–8.0 in SL (7.8 in holotype of *A. chaplini,* 5.7–7.2 in holotypes of remaining species); head length 4.5–5.0 in SL (3.0–4.4 in other species).

Cephalic sensory pores: mandibular 4; common 1; preopercular 5; posttemporal 2–3; lateral supratemporal 2–3; median supratemporal 1–2; supraorbital 1–3; posterior infraorbital 3; anterior infraorbital 3; frontal 0–1; median interorbital 1–3; anterior frontal 1.

Supraorbital cirrus complexly arborescent; main stalk usually comprising three palmate, multifid branches—a large central branch with two smaller branches arising proximally on either side of it; medial to main portion of cirrus, a smaller multifid branch arises at posterolateral margin of stalk base; cirrus generally longer in males (1–1.8 in eye) than in females (1.5–2.0 in eye). Anterior nostril on short tube, with posterior rim extended as multifid cirrus (length 1.2–2.2 in eye of males, 2.0–2.6 in eye of females).

Dorsal fin with fleshy flap on anterior margin of first spine. Membranes between adjacent spines and soft rays of dorsal fin not notably incised, continuous between tips of elements so that margin of fin is smooth; last spine slightly shorter than first soft ray, resulting in slight notch at junction of spinous and soft portions of fin. Membranes between adjacent rays of anal fin incised, extending posteriorly from tip of each ray of anterior margin of succeeding ray slightly proximal to tip, so that tip of each ray appears slightly exerted; exerted tips of all rays curved posteriorly; condition exaggerated in males wherein tissue surrounding ray tips is notably thickened. Ultimate dorsal- and anal-fin rays connected along caudal peduncle by membrane that extends to distal tips of posteriormost dorsal and ventral procurrent caudal rays. Margin of caudal fin rounded. Pectoral fin large, rounded, with weakly scalloped margin; ventralmost three rays thicker than others and with tips slightly exerted, more so in males.

Vomerine teeth 9–13, arranged in ring, frequently with one tooth in center. Each palatine with two rows of teeth, 3–7 in outer row, 1–4 in inner row (one specimen has only 3 in single row on one palatine). Each premaxilla with outer row of 8–12 teeth, flattened and pointed at tips, becoming less so posteriorly as they also decrease in size, and inner band of smaller, curved, conical teeth. Anterior expanded portion of each dentary with outer row of 7 relatively incisiform teeth, similar in configuration to outer row on premaxillae, and inner band of smaller, robust, conical teeth that continue as single row onto straight, posterior portion, where they become considerably larger. Gill rakers 3+5.

Anterior and dorsal areas of head ornamented with anteriorly directed spines (Fig. 2). Supraorbital rim of each frontal bearing row of five to six spines that extends from posterodorsal corner of orbit anteriorly to junction with lateral ethmoid and nasal where a row of spines continues on each of these bones. Each lateral ethmoid bears two spines on anterior orbital rim. Each nasal bears four spines, a vertical row of three and one lateral to the ventralmost of these. Each lacrimal bears four to five spines along anterior half of dorsolateral margin, these decreasing substantially in size posteriorly. Dorsum of cranium (frontals) with a roughly diamond-shaped patch of 17–23 spines, its anterior apex extending just anterior to a point about midway between posterior orbital rim and pupil, or slightly beyond, and its posterior apex reaching posteriorly about two-thirds distance between posterior orbital rim and dorsal-fin origin.

Color in alcohol.—Background coloration over head and body is uniformly pale cream to straw. Pigmentation is sparse and extremely variable among individuals. In

addition to the intrinsic individual variability, it appears that there is substantial loss of dark pigment with time in alcohol. The FMNH specimens (all in alcohol for at least ten years) exhibit only a sparse distribution of black pigment. Fresher specimens (USNM material, preserved for about one year) exhibit the dark black melanophores that characterize the older material, but also have large numbers of fine, purplish-red pigment cells. The latter are apparently lost with long-term storage in alcohol. Due to the marked differences, FMNH and USNM specimens are described separately.

FMNH specimens: Posterior to the anus, the body surface is immaculate, although in some specimens a few internal clusters of melanophores can be detected along the vertebral column. Anterior to the anus, the amount and arrangement of external melanophores varies considerably; some individuals appear almost completely devoid of pigment, and there is no consistent pattern of melanophores and no consistent sexual dichromatism. The following description emphasizes the most consistent pigmentary features. There are frequently two sparse clusters of internal melanophores in the ventrolateral area of the abdominal cavity just anterior to the anus; melanophores also may be scattered variously along the mid-ventral and ventrolateral surfaces of the anterior portion of the abdominal cavity, in the area below the pectoral fin. The abdominal pigmentation frequently consists of two posterodorsally directed crescents, one just anterior to the anus and the other just ventral to the pectoral fin. Small individual melanophores occasionally occur on the dorsal half of the body surface, usually anterior to a vertical from the anus. Branchiostegal rays and membranes may be unpigmented, or covered with scattered or densely packed melanophores; ventrally, the anterior rays are more heavily pigmented, but in some specimens melanophores also occur at the dorsal tips of the most posterior rays, where they curve an-

teriorly above the opercle. In occasional specimens, there are a few melanophores on the cheek just anterior to the angle of the preopercle. The iris is uniformly black, otherwise the head lacks pigment. The pectoral fin may be immaculate, have a sparse sprinkling of melanophores, or have a more regular arrangement of melanophores along the dorsal and ventral edges of many of the rays, the latter usually being denser on the medial side of the fin; in a few specimens the ventral portion of the pectoral-fin base is pigmented. The pelvic-fin base and rays range from immaculate to relatively heavily pigmented. Frequently there are several sparse clusters of melanophores irregularly placed along the spinous dorsal fin, more or less associated with the more distal portions of individual spines; these sparse clusters begin posterior to the fifth spine, but in occasional specimens there is a larger, denser concentration of pigment on the membrane between the third and fourth spines. Dorsal soft rays are more consistently pigmented, most specimens having many rays with several mostly dash-like melanophores lying along their anterior and/or posterior edges. Similar pigment occurs much less frequently on the anal-fin rays. Most caudal-fin rays have dash-like melanophores along their dorsal and ventral edges.

USNM specimens: The melanophore patterns described above also characterize the fresher USNM specimens and will not be repeated here, where we describe only the additional purple-red pigment cells, referred to, for convenience, as "P-phores." Both the persistent black melanophores and the transient P-phores are evident in the black-and-white photograph of the holotype (Fig. 1), where the dichotomy is evidenced to some extent in relative intensity of the spots. In fresh, unpreserved specimens, there is no detectible dichotomy, that is, all dark pigment cells appear black. Soon after formalin fixation, the majority of these dark spots fade to purplish-red and, with long-term storage in alcohol, apparently
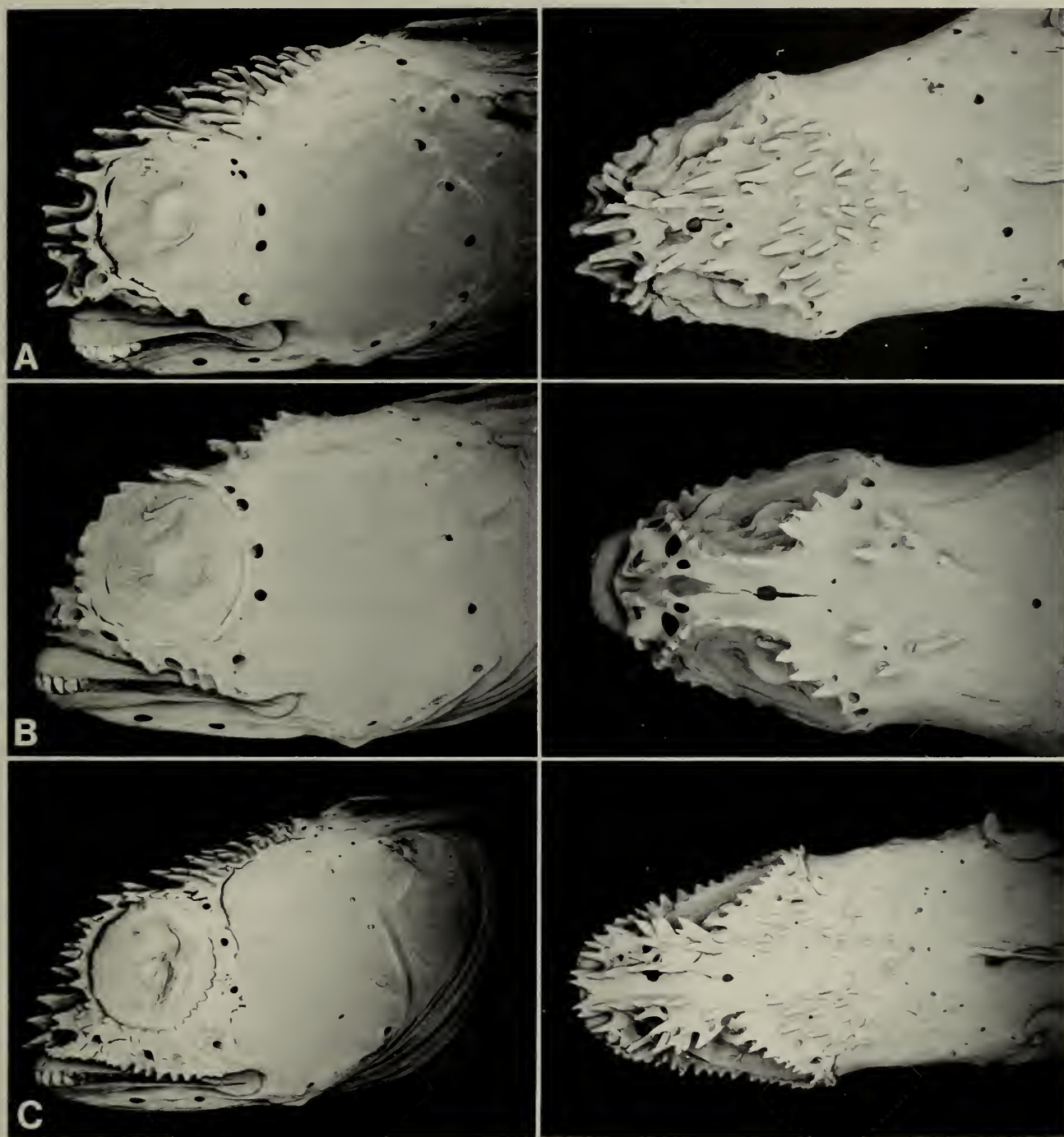
Fig. 2.   Scanning electron micrographs illustrating head spines and cephalic sensory pores of three species of *Acanthemblemaria* in lateral (left) and dorsal (right) views; all males, supraorbital cirri removed. (A) *A. paula,* FMNH 90876, 15.4 mm SL; (B) *A. aspera,* USNM 276052, 19.1 mm SL; (C) *A. spinosa,* USNM 198276, 21.6 mm SL.

continue fading, eventually disappearing to leave only the black melanophores described above. (In rare specimens some pigment cells with distributions characteristic of P-phores appear black.) In all specimens, a fine speckling of P-phores begins in the pectoral region of the body at about the level of the sixth to eighth dorsal spine and ex-

tends anteriorly to cover much of the head, including the opercular series, branchiostegal membranes, pectoral-fin base and about half the surface of the fin, pelvic-fin base and rays and, in some specimens, the membrane between the first four or five dorsal spines. The densest concentration of P-phores is seen on the branchiostegal

membranes of some males; females tend to have this area more lightly pigmented, but this sexual difference is inconsistent. On the head, the most sparsely pigmented areas are the cheek, anterior portion of the cranium, and the jaws, which are frequently immaculate; denser concentrations are found just posterior and ventral to the orbit, forming one or two oblique bars. Superficial and subcutaneous P-phores may also be apparent on the abdomen, where they may be associated with the two distinctive crescents described for the melanophores. Dorsal to these, one or two small clusters of superficial P-phores occur on the upper body in some specimens. Deep, internal blocks of P-phores may be present on six to eight centra along the length of the body, and, in such specimens, there are usually clusters of P-phores at the bases of every second or third dorsal- and anal-fin ray. These clusters begin internally around the pterygiophores and may rise to the surface at the fin-ray bases, sometimes extending a short distance along the rays. P-phores are also found along the bases of some caudal-fin rays.

In USNM specimens that were retained in formalin for several months before transfer to ethanol, white pigmentation (leucophores) is evident in discrete patches on the head, fins, and body. There is a prominent white patch or oblique bar, bordered by the two purple-red bars, on the lower portion of the cheek immediately posterior to the orbit. There is a triangular white patch on the dorsum of the cranium between and immediately posterior to the orbits, the iris is white with a speckling of P-phores, and the supraorbital cirrus is white. Several discrete white patches occur on the opercular series and branchiostegal membranes, and the entire gular region is white. Leucophores are also prominent on the pelvic-fin rays and the pectoral-fin base and proximal one-third or more of the fin. Large areas of white pigment may be seen internally on the abdomen, and smaller superficial clusters may be seen on the body dorsal to this. The

membrane between the first four to seven dorsal spines is white. Internal and superficial leucophores at the bases of dorsal- and anal-fin rays alternate with the similarly placed P-phores described above.

Live color.—The following description is based on specimens that were placed on ice while still alive, painted with full strength formalin to fix the fins, and photographed immediately thereafter. All pigment described above is evident, but, as noted, melanophores and P-phores are indistinguishable. The head and anterior body (to about the anus), including the pelvic and proximal portion of the pectoral fins, appear predominantly white with prominent black and greenish-yellow (xanthophores) markings. Two distinctive black crescents are evident on the silvery-white background of the abdomen. Xanthophores are in close association with melanophores (and P-phores), so that their distribution is essentially completely overlapping. The large white blotch covering the anterior portion of the spinous dorsal fin is a very prominent feature. Posterior to the anus, the body is transparent with alternating white and dark markings along the lateral midline and median fin bases. Most distinctive is a series of seven to eight rectangular blocks of white pigment lying internally along the vertebral column, each encompassing two to four centra. These white blocks are bordered on either side by narrower, less circumscribed, dark greenish marks that frequently extend to the bases of the dorsal and anal fins.

Sex.—Specimens are easily sexed based on genital morphology. Males have a single papilla at the posterior margin of the anus, whereas in females the anus is surrounded by a papillar fringe. The ratio of males to females in both the USNM and FMNH collections is about two to one. Because most specimens were collected individually with quinaldine, we cannot discount the possibility that the sex ratio is partially a reflection of collecting bias. Nonetheless it seems likely that males significantly outnumber fe-

males in the natural population. Greenfield & Greenfield (1982) reported that males of *Acanthemblemaria spinosa* and *A. greenfieldi* significantly outnumbered females in their collections, and Rosenblatt & Stephens (1978) reported that sex ratios in their collections of *Mccoskerichthys sandae* was strongly biased in favor of males.

There appears to be no pronounced sexual dimorphism; however, as described above, males tend to have slightly larger supraorbital and nasal cirri and usually have the tips of the anal-fin rays notably thickened and more strongly curved. Males also tend to have more intense and extensive dark pigmentation on the branchiostegal membranes than do females, but this is not a consistent difference. Males ranged in length from 10.1 mm to 18.4 mm with a mean of 14.8 mm, whereas females ranged from 10.3 mm to 16.7 mm with a mean of 13.1 mm. Size at sexual maturity and fecundity are discussed below.

Etymology.—*Paula*, Latin for little, in reference to the diminutive size of this fish, the smallest member of the Chaenopsidae, here used as a noun in apposition. The name was chosen to honor Paula Keener, who participated in the collection that resulted in recognition of this species.

Habitat.—*A. paula* occupies burrows made by invertebrates (usually those of sipunculids) in dead coral in shallow water (<5 m) on both sides of reef crest and on pavement zone of reef flat.

Distribution.—Known only from the barrier reef and outlying atolls of Belize.

Material examined.—114 specimens (10.1–18.4 mm) in 20 collections, all from Belize.

Holotype.—USNM 301835, 15.9 mm male taken with quinaldine from dead coral on reef flat at south end of Carrie Bow Cay, Belize, at depth of 1–2 m on 22 Mar 1988, by G. D. Johnson, and party.

Paratypes.—Carrie Bow Cay. South end of island, depth 1.0–2.5 m, coral rubble and pavement zone on reef flat: FMNH 90876

(17, 13.8–18.4, 3 prepared for SEM), 4 Jan 1978, D. W. and T. A. Greenfield, and C. Rakocinski; FMNH 90869 (8, 12.9–16.6), 17 May 1977, D. W. and T. A. Greenfield; USNM 301831 (3, 13.1–16.7), 21 Mar 1988, G. D. Johnson; USNM 301836 (4, 13.4–15.1), 22 Mar 1988, E. B. Brothers, R. A. Fritzsche, and G. D. Johnson; USNM 301832 (10, 11.6–17.0), 25 Mar 1988, G. D. Johnson; ANSP 162806 (6, 11.8–16.0), 26 Mar 1988, G. D. Johnson; USNM 301833 (23, 12.1–16.7), 28 Mar 1988, R. A. Fritzsche and G. D. Johnson; SIO 89-14 (1, 15.4), 19 Nov 1988, R. A. Fritzsche; SIO 89-13 (5, 11.6–15.3), 19 Mar 1989. North end of island, coral and coral rubble just outside reef crest, 2–5 m: USNM 290669 (2, 12.4–14.9), 24 Mar 1987, E. B. Brothers, G. D. Johnson, and P. Keener; USNM 301834 (9, 10.3–15.2, cleared and stained), 17 Mar 1988, E. B. Brothers, R. A. Fritzsche, G. D. Johnson, and P. Keener. East side of island, just inside reef crest, 1–2 m: FMNH 98298 (3, 13.9–15.0), 16 May 1977, D. W. and T. A. Greenfield; USNM 301830 (3, 10.8–14.7), 27 Mar 1988, E. B. Brothers, R. A. Fritzsche, and G. D. Johnson. Collection site unspecified: FMNH 89372 (1, 14.8), 2 Jan 1978, D. W. Greenfield et al.; FMNH 89328 (2, 15.2–15.8), 14 May 1977, D. W. Greenfield.

Glover's Reef. Cay in shallow water behind cabin no. 9: FMNH 90497 (12, 12.0–15.5), 14 Jun 1978, G. Glodek, D. W. Greenfield, and R. K. Johnson. West side of Long Cay, about 200 yards south of cabin no. 9: FMNH 98296 (1, 14.2), 9 Jun 1978, G. Glodek and T. Murphy. Collection site unspecified: FMNH 77558 (1, 13.5), 29 Jul 1973, D. W. and T. A. Greenfield.

Buttonwood Cay. One mile south of island: FMNH 86085 (3, 11.7–13.6), 23 Jul 1974; FMNH 86088 (1, 10.1), 23 Jul 1974.

Sargeant's Cay. FMNH 98297 (2, 11.6–12.4).

Ambergris Cay. 2.5 miles north of San Pedro: FMNH 98295 (1, 14.8).

Discussion.—A cladistic analysis of rela-

tionships within *Acanthemblemaria* is beyond the scope of this study. Furthermore, although Stephens' (1963) surmise that *Ekemblemaria* is the closest relative of *Acanthemblemaria* seems reasonable, character polarity for *Acanthemblemaria* remains problematic in the absence of a well-corroborated cladistic hypothesis of generic relationships for the Chaenopsidae. Based on unpolarized similarities, we believe that *A. paula* is probably most closely related to *A. aspera* and *medusa*, two species that Smith-Vaniz & Palacio (1974) hypothesized to be closely related, but this remains to be tested cladistically. These three species (*paula, aspera* and *medusa*) share complex, deeply branched supraorbital cirri not found in other members of the genus. Head spines in *A. paula* are long as in *A. maria* and *spinosa* but not as numerous. Distribution of spines on top of the head is more like that in *A. aspera* and *medusa*, wherein there is a triangular patch on the frontals extending posteriorly from the orbits. In *paula* this area is completely covered with spines, whereas in *aspera* and *medusa* it is largely smooth (Fig. 2). The extreme development of fleshy papillae that uniquely characterizes *A. medusa* is lacking in *paula*, and several characters suggest that *paula* and *aspera* are most closely related. They share the lowest dorsal-fin spine count in the genus ($\bar{x}$ = 19.2 and 20.5, respectively; 21.7 in *medusa*) and the lowest segmented caudal-fin ray count among Atlantic species ($\bar{x}$ = 12.4 and 12.3; 13.0 in *medusa*; data not available for eastern Pacific species). Finally, the color patterns of *A. paula* and *aspera* resemble one another more closely than they do that of any other species. Preserved specimens lack any regular external pigment pattern consisting of repeated bars, stripes or spots.

Acanthemblemaria paula may mature at sizes smaller than any known blennioid, although data in size at sexual maturity is lacking for most species. Females of *A. paula* may be ripe at 11.5 mm and individuals smaller than 11.0 mm may have developing

eggs. Among the smallest known blennioids are the blenniid, *Medusablennius chani* (Springer, 1966) and the labrisomid, *Starksia nannodes. Medusablennius chani* is known from ten specimens ranging in size from a 12.1 mm ripe female to a 15.4 mm immature male (Smith-Vaniz & Springer 1971). Specimens of *S. nannodes* examined by Bohlke & Springer (1961) ranged from 10.5 to 17.0 mm with a 13.1 mm ripe female. There is little published information on size at sexual maturity in chaenopsids, but all species attain maximum sizes larger than *A. paula* (18.4 mm). Within *Acanthemblemaria*, specimens 30 mm or longer (some >50 mm) are known for all 15 species. Whatever the precise relationships of *A. paula* to other species of the genus, its small size is unquestionably derived.

Weitzman & Vari (1988) listed 85 species representing five orders and 11 families of miniature Neotropical freshwater fishes. Miniature species were considered by Weitzman and Vari to be those that either are known to mature sexually at less than 20 mm and may reach slightly larger sizes (<25–26 mm), or for which maturity data are unknown but which are not reported to exceed 25–26 mm in the wild. By those criteria, *Acanthemblemaria paula* is unequivocally a miniature species. The elongate body and relatively small head further emphasize its miniature stature; wet weights of 15 specimens, 13.4–16.4 mm in length, ranged from a mere 15 to 25 mg.

Weitzman & Vari (1988) noted that all species in their list of miniatures that had been examined in detail exhibit numerous apparently paedomorphic morphological reductions, particularly in the degree of development of the laterosensory canal system of the head and body, sculpturing on the bones of the head and total numbers of fin rays and body scales. The state of these and other characters in *A. paula* indicates that miniaturization does not always involve obvious reductive paedomorphic expression. The laterosensory ossifications

and pores (Fig. 2) of *A. paula* appear no less developed than in other species of the genus. Head spination is among the most extensive in the genus and considerably more pronounced than that of *A. aspera,* the putative closest relative, which reaches a maximum size of about 35 mm. Total numbers of dorsal- and anal-fin rays are lower than those of some species but higher than others and not reduced compared to those of *aspera.* Stephens (1963) also noted the lack of correlation between reduced body size and numbers of dorsal- and anal-fin rays among other species of *Acanthemblemaria.* Pectoral-fin ray counts do not differ substantially among species of *Acanthemblemaria,* and all chaenopsids lack scales, so no intrageneric comparisons of states of these characters can be made. We have identified only two features (neither absolute reductions) of *A. paula* that might be interpreted as paedomorphic. Although the total number of dorsal-fin elements is equal to that of *aspera, paula* has one more soft ray and one fewer spine; in fact, the mean dorsal-fin spine number (19.2) is the lowest in the genus. If transformation of the posteriormost dorsal-fin spines from soft rays occurs ontogenetically in chaenopsids, as it does in many percomorphs, the dorsal-fin ray composition of *A. paula* could be interpreted as paedomorphic with respect to the other species. The very slender, elongate body of *A. paula,* equalled in only one other species, *A. chaplini,* could also be seen as paedomorphic, because chaenopsid larvae are relatively more elongate than adults. It seems clear that the marked reductive features that characterize miniaturization in Neotropical freshwater fishes and at least some marine fishes (e.g., some gobioids, Springer 1983, 1988), are not universally associated with extreme size reduction.

In a study of habitat and resource partitioning between *Acanthemblemaria spinosa* and *A. greenfieldi,* Greenfield & Greenfield (1982) compared ecological and life history parameters of the two species. All subse-

quent references herein to G&G pertain to that paper. They found that *A. spinosa* occurs only on horizontal surfaces of dead coral whereas *A. greenfieldi* occurs only on vertical surfaces, but they noted an apparent exception in their collections. One collection made in a typical *A. greenfieldi* habitat (coral rubble and pavement zone of the back reef) contained, in addition to 36 specimens of *A. greenfieldi,* 17 specimens identified as "young *A. spinosa.*" Catalog numbers were not given, but based on the date, locality and number of specimens, we conclude that that collection is FMNH 90869, which consists of 17 specimens of *A. paula.*

A total of 90 specimens identified as *A. spinosa,* collected at Carrie Bow Cay 10–17 May 1977 and 1–4 Jan 1978, were analyzed by G&G for length frequency, stomach contents and fecundity. Of these, 30 are actually *A. paula.* Consequently, most of G&G's conclusions about life history parameters of *A. spinosa* are invalid. We did not attempt to reanalyze their data, because all 90 specimens were not used in determining each parameter and we were unable to determine how many *A. paula* were included in each analysis. Most profoundly affected are the data on size at sexual maturity and fecundity. Their observation that *A. spinosa* females mature as small as 12.4 mm is clearly based on specimens of *A. paula.* We examined 25 female *A. spinosa,* ranging in size from 11.6 to 20.4 mm; the smallest ripe individual was 15.6 mm and the mean size of ripe individuals was 18.4 mm. Of 22 female *A. paula,* 10.3–16.7 mm, the smallest ripe specimen was 11.5 mm, and the mean size of ripe specimens was 13.6 mm.

Conclusions regarding average brood size in *A. spinosa* were also affected by inclusion of several specimens of *A. paula.* Based on data presented in fig. 218 of G&G, the number of eggs per brood in *A. spinosa* ranged from 5 to 25 with a mean of 12.8. If specimens smaller than 15 mm (presumably all *A. paula*) are removed from the data, brood size ranges from 8 to 25, with a mean of

14.8. This probably still includes some specimens of *A. paula,* in which the brood size is substantially smaller, but is in better agreement with our own data from ten specimens of *A. spinosa* with a range of 9 to 30 and a mean of 17.2. Among sixteen specimens of *A. paula,* numbers of eggs per brood ranged from 1 to 10, with a mean of only 4.7. This conforms with our single observation of eggs in a burrow of a male *A. paula*; the clutch consisted of only four eggs, all apparently close to hatching. The egg size of *A. paula* and *spinosa* is roughly the same with the largest eggs averaging 0.7–0.8 mm in diameter.

Misidentification of *A. paula* led G&G to the following speculation about larval recruitment in *Acanthemblemaria*:

The 4 January 1978 collection from a typical *Acanthemblemaria greenfieldi* habitat, which also yielded young of *A. spinosa,* provides valuable information concerning the interactions of these two species. Although the adults exhibit complete habitat separation, apparently planktonic larval *Acanthemblemaria* species settle and occupy any available hole or crevice. Because individuals of *A. spinosa* found here were only 18.4 mm or less, it may be assumed that when they outgrow their holes and search for a larger hole, they are excluded by *A. greenfieldi* from this habitat.

Because the young *A. spinosa* referred to above are actually adult *A. paula,* these conclusions are unsubstantiated. There is no evidence that individuals of *A. spinosa* occupy the specific *A. greenfieldi* habitat at any stage of their lives. In contrast, individuals of *A. paula* occupy this habitat throughout their lives and are not excluded by *A. greenfieldi* as they grow; in fact, the specific collection referred to by G&G contains the two largest known specimens of *A. paula.* Coexistence is undoubtedly facilitated by the fact that the diminutive *A. paula* utilizes small burrows that are unavailable to the much larger adult *A. greenfieldi*; according

to G&G, *A. greenfieldi* matures at 19.0 mm (almost twice the size for *A. paula*) and reaches a maximum size of 32.5 mm with mean sizes of 25.5 and 23.5 for males and females, respectively. Thus, although adults of *A. paula* may compete for space with newly settled or juvenile *A. greenfieldi,* there is fine-grain habitat (refuge) partitioning between adults of the two species. This would be worth further investigation with respect to the findings of Stephens et al. (1970) on *Hypsoblennius jenkinsi.* Those authors found that maximum size of individuals was controlled by size of available tubes and hypothesized that individuals that outgrew the available tubes were subject to a greater risk of predation.

Our observations at Carrie Bow Cay on the microhabitat distribution of *A. paula* and *greenfieldi* failed to establish a clear-cut specificity to either vertical or horizontal surfaces; in areas where both surfaces were abundant, both were occupied. In a single collection (19 Mar 1989) using quinaldine just inside the reef crest we took: 7 specimens of *greenfieldi* and 8 of *paula* from vertical surfaces; 6 of *greenfieldi* and 13 of *paula* from oblique surfaces; and 2 of *greenfieldi* and 8 of *paula* from horizontal surfaces. We found these two species limited to horizontal surfaces only far back on the reef flat, where vertical surfaces are much less prevalent. *Acanthemblemaria spinosa* does not occur far inside the reef crest and appears to live primarily on vertical surfaces. Discussion by G&G of competitive interaction and displacement among *Acanthemblemaria* species is speculative and not supported by evidence that shelter is a resource limiting population size. Hastings (1984) demonstrated the latter for *A. crockeri,* and similar experimental field manipulations of the habitat and/or fishes will be necessary to elucidate the nature of interspecific interactions between the species in question here. G&G made a valuable contribution by emphasizing and reviewing the potential significance of very subtle differences in habitat utilization in small, cryptic reef fishes.

Fish community ecologists have shown an understandable bias for larger and more conspicuous fishes such as wrasses, damselfishes, surgeonfishes, butterflyfishes, etc. Population and behavioral characteristics of such groups may be entirely different from those of the diminutive, cryptic and frequently speciose blennies, gobies, eels, ophidioids, dactyloscopids, etc. Although some work has been done on chaenopsids and other blennies (e.g., Lindquist 1985, Stephens et al. 1966, Wirtz 1983), we remain largely ignorant of the demography, life history and recruitment biology of such fishes.

The very small size of *Acanthemblemaria paula* and some of its congeners raises a number of interesting questions, particularly with respect to longevity, fecundity and larval ecology. How can such species maintain populations when females apparently produce so few eggs in a lifetime? *Acanthemblemaria* species lay demersal eggs that presumably hatch to a planktonic larval stage. Based on otolith microstructure (Brothers et al. 1983) we have made preliminary determinations of the planktonic duration of the larvae of four species in the genus (*paula, aspera, greenfieldi, spinosa*). All show stereotypic "settlement marks" at presumptive ages of 22 to 25 days. A larval period of this magnitude is equal to or longer than that exhibited by many larger reef species having instantaneous fecundities hundreds to many thousands of times greater (e.g., Brothers & Thresher 1986). Do these chaenopsid blennies have any special ecological and/or behavioral adaptations that reduce larval mortality in the plankton? Do they bypass the planktonic phase completely? Detailed life history studies of small, short-lived reef species will undoubtedly yield many surprises.

Acknowledgments

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